American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N. Y. 10024

NUMBER 2315 FEBRUARY 28, 1968

The Genus *Proterix* (Insectivora, Erinaceidae) of the Upper Oligocene of North America

By Constance Elaine Gawne[1]

INTRODUCTION

The type specimen of *Proterix loomisi* was collected by F. B. Loomis in 1902 and described by Matthew in 1903 as a true hedgehog of the subfamily Erinaceinae. Butler, in 1948, considered it an isolated form which might be an offshoot of the Erinaceinae. Since that time two more specimens of *P. loomisi* have been found: a fragment of a right ramus tentatively referred here by J. R. Macdonald (1961), and a specimen collected from the Whitney of Nebraska in 1956 by Morris F. and Shirley Marie Skinner of the Frick Laboratory. This specimen was contained in a nodule, and consists of the nearly complete right ramus, part of the left ramus, part of a premaxilla and other skull fragments, a mold from which a latex cast showing the dentition was made, and two vertebrae.

In 1951 J. R. Macdonald described an insectivore skull, collected from the Poleslide member of the Brule Formation in 1940 by James D. Bump, naming it *Apternodus bicuspis*. Further study, particularly of the tympanic region, which has been cleaned since the skull was first described, shows it to be an erinaceid, although it possesses extensive posterolateral plates, here called lambdoid plates, resembling those of *Apternodus*. It has ossified bullae made up of wings of the alisphenoid,

[1] Department of Geology, Columbia University.

basisphenoid, and periotic, whereas *Apternodus* does not have ossified bullae. A fragment of matrix preserves the impression of a strong zygomatic arch; *Apternodus* has none. The dentition of *Apternodus* is zalambdodont; this specimen has an erinaceid P^4 (described as P^3 by Macdonald) resembling P^4's of *Galerix* and of *Neurogymnurus,* and especially the lingual part (all that is preserved) of the P^4 of *Proterix loomisi.*

Another specimen referable to this species was found in the Whitney of Nebraska by Morris F. Skinner in 1952. This consists of two rami, with the dentition nearly complete, part of a maxilla, and eight vertebrae.

Comparison of *"Apternodus" bicuspis* with *Proterix loomisi* shows many similarities, and the differences that exist seem insufficient to justify separation at the generic level. I therefore transfer this species to *Proterix.*

I wish to express my gratitude to Dr. Malcolm C. McKenna for much valuable advice, criticism, and encouragement during this study; to Dr. Robert W. Wilson of the South Dakota School of Mines and Technology for the loan of specimens and for stratigraphic information; to Mr. Morris F. Skinner of the Frick Laboratory for stratigraphic information; to Dr. Frederick S. Szalay for taking the photographs; and to Mr. Raymond Gooris of the Frick Laboratory for making the drawings.

The following abbreviations are used with catalogue numbers:

A.M.N.H., the American Museum of Natural History
F:A.M., the Frick Laboratory in the American Museum of Natural History
S.D.S.M., the South Dakota School of Mines and Technology, Rapid City

SYSTEMATICS

ORDER INSECTIVORA ILLIGER, 1811

SUPERFAMILY ERINACEOIDEA GILL, 1872

FAMILY ERINACEIDAE BONAPARTE, 1838

SUBFAMILY UNCERTAIN

PROTERIX MATTHEW, 1903

TYPE: *Proterix loomisi* Matthew, 1903.

INCLUDED SPECIES: The type species, and *Proterix bicuspis* (Macdonald, 1951).

KNOWN DISTRIBUTION: Whitneyan of South Dakota and Nebraska.

DIAGNOSIS: Erinaceids with the anterior part of the skull short; palate completely ossified; well-developed supraorbital crests and postorbital processes, and temporal crests uniting just behind the orbits to form a strong sagittal crest; premaxillae not meeting frontals; elongate nasals

extending posterior to the postorbital processes; deep depressions anterior to the orbits for the snout musculature; strong zygomatic arches; extremely large, completely ossified bullae; massive, flat, vertical lambdoid plates; no basisphenoid pit; vertebrae with their sides covered by large, overlapping, vertical plates; number of upper and lower premolars reduced; P^3–M^3 three-rooted; small triangular M^3; M^1 quadrate, large, with subequal paracone and metacone, subequal protocone and hypocone, small metaconule, small metastylar crest, and a crest extending anterobuccally from the protocone; P^4 with large paracone, short, strong metastylar crest, and protocone with small hypocone appressed to it; upper canine large and two-rooted; I_1^1 enlarged; I_2 (and I_3 if present) procumbent; lower canine long, peglike, and procumbent; P_2, if present, small, simple cone; P_3 small, with posterior cingulum; P_4 large, with large protoconid, small paraconid crest on its anterior face, and narrow talonid; M_1 five-cusped, with low, elongate paraconid; M_2 and M_3 four-cusped, with a broader cingulum in place of the paraconid; talonids of all molars relatively short anteroposteriorly, with hypoconid and entoconid large and well separated; talonids of M_1 and M_2 about as wide transversely as trigonids, talonid of M_3 narrower; large mental foramen below anterior root of P_4; dentary deep and stout.

Proterix loomisi Matthew, 1903

Type: A.M.N.H. No. 9756.

Type Locality and Horizon: Indian Draw, Cheyenne River, South Dakota, in the upper Oreodon beds.

Referred Material: S.D.S.M. No. 55140, from S.D.S.M. locality V5411, Rosebud locality 33 (see Macdonald, 1963), Godsell Ranch, S. $\frac{1}{4}$ sects. 11 and 12, E. $\frac{1}{2}$ sect. 14, W. $\frac{1}{2}$ sect. 13, Shannon County, South Dakota; Oligocene horizons just below ash in the Leptauchenia nodules.

F:A.M. No. 74962, "from one-half mile south of Sheridan Gate Buttes in western Sheridan County, Nebraska. Also about 10 miles east and a little north of Chadron, Nebraska. Zone: about 20 feet below base of gray zone that looks like a channel and 65 feet or more below what we believe to be the lower ash in the Whitney Formation as shown at the Augustine locality about two and one-half miles to the southwest" (Skinner, MS).

Known Distribution: Whitneyan of Nebraska and South Dakota.

Diagnosis: P_2^2 present; I_3^3 present; protocone present on P^3; P^3 about two-thirds of height of P^4; hypocone of P^4 larger than in *P. bicuspis;* paraconid crest and talonid of P_4 larger; M^1 shorter anteroposteriorly; M^2 quadrate; M^2 and M^3 larger relative to M^1 (table 1); palate ex-

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF DENTITION OF *Proterix*

	P^4	M^1	M^2	M^3	P_4	M_1	M_2	M_3
Proterix loomisi								
A.M.N.H. No. 9756								
Right								
Width	4.0[a]	4.7	3.9	2.5	—	—	—	—
Length	3.2[a]	3.4	2.9	—				
Left								
Width	—	4.7	3.9	2.8	—	—	—	—
Length	3.3	3.4	2.9	2.1	—	—	—	—
S.D.S.M. No. 55140								
Width	—	—	—	—	2.7	3.4	—	—
Length	—	—	—	—	3.2	4.2	—	—
F:A.M. No. 74962								
Right								
Width	—	—	—	—	2.2	—	—	—
Length	—	—	—	—	2.9	—	3.1[a]	—
Left								
Width	—	—	—	—	2.2	3.1	—	—
Length	—	—	—	—	2.9	3.8	3.0	2.6
Proterix bicuspis								
S.D.S.M. No. 4048								
Width	5.3	5.1[b]	—	—	—	—	—	—
Length	4.0	4.9[b]	—	—	—	—	—	—
F:A.M. No. 74961								
Right								
Width	4.3	4.7	—	—	2.8	3.1	3.1	2.2
Length	3.5	4.3	—	—	3.2	3.9	3.5	—
Left								
Width	—	—	—	—	2.6	3.1	3.1	2.2
Length	—	—	—	—	3.0	4.0	3.4	2.6

[a] Damaged.
[b] From alveolus.

tending farther behind M^3; zygomatic arch arising opposite M^2, and not so deep vertically; shorter orbitotemporal region; and bullae not quite so large. Most of the posterior part of the skull is unknown.

REMARKS: Matthew's description of the type (1903) needs little comment, except to point out that his statement that P^4 was molariform was based on the presence of two large buccal roots, the outer cusp of the tooth on each side being broken away. Also, he did not mention the large groove present on each side of the median suture of the palate and about 0.5 mm. from it. This specimen is illustrated in the present

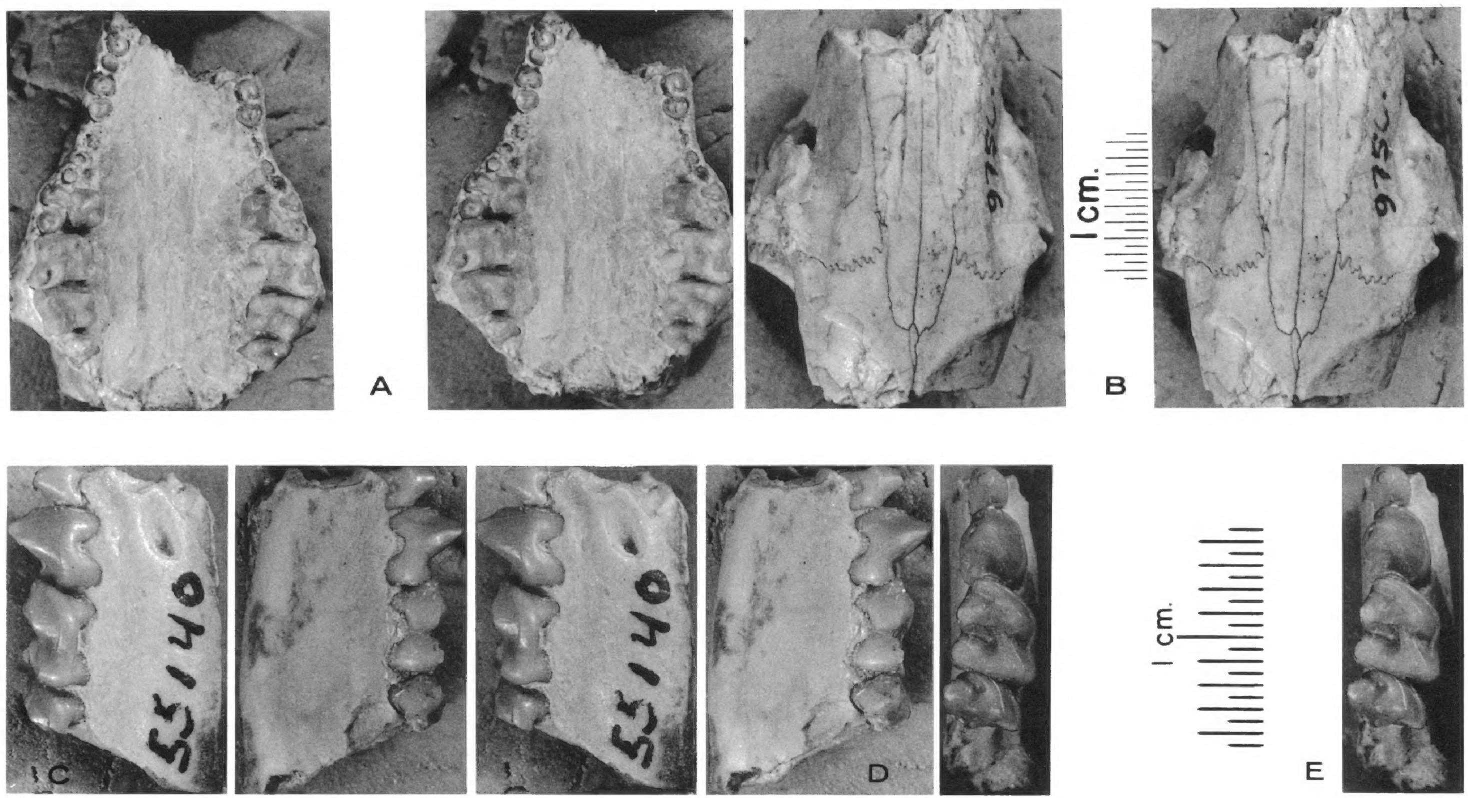

FIG. 1. *Proterix loomisi.* A, B. Type, A.M.N.H. No. 9756. A. Palatal view. B. Dorsal view. ×2. C–E. S.D.S.M. No. 55140, partial right ramus, with P_3–M_1 and trigonid of M_2. C. Buccal view. D. Lingual view. E. Occlusal view. ×3.

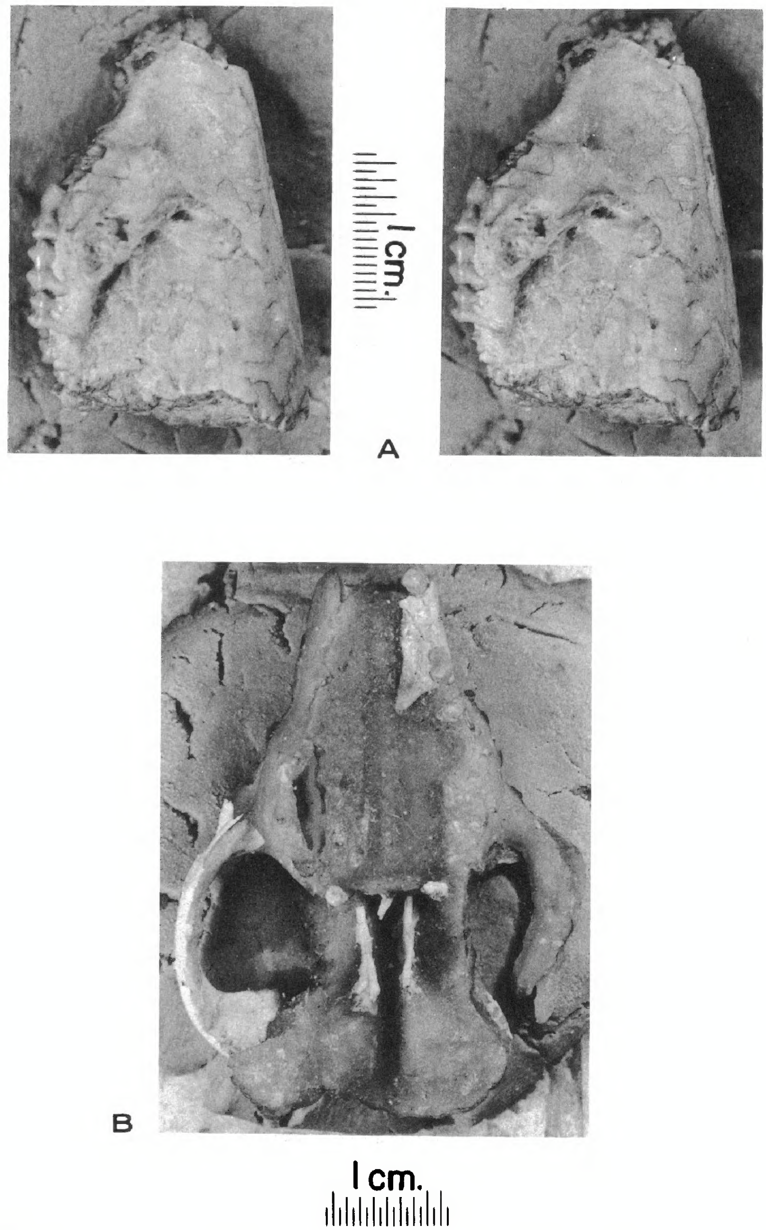

FIG. 2. *Proterix loomisi.* A. Type, A.M.N.H. No. 9756, lateral view. ×2. B. F:A.M. No. 74962, partial latex cast of skull, with bone fragments added, palatal view. ×1.5.

paper (figs. 1A, B, 2A). New measurements made on the type, agreeing well with his, are given in table 1.

Macdonald's description (1961) of S.D.S.M. No. 55140 is also good, but I should mention that he gave the length of P_3 as 1.90 mm., which is 1.4 mm. longer than is shown by new measurements. This specimen is shown here in figures 1C, D, E, and 3.

The third specimen of *P. loomisi* (F:A.M. No. 74962) was collected by the Skinners in 1956. Part of the ventral side of the skull of this specimen is represented by a latex cast taken from the nodule in which the

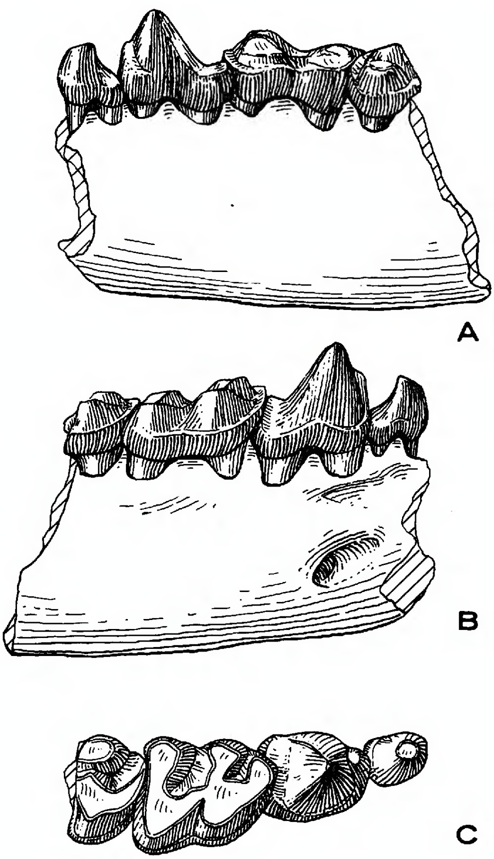

FIG. 3. *Proterix loomisi,* partial right ramus, with P_3–M_1 and trigonid of M_2, S.D.S.M. No. 55140. A. Lingual view. B. Buccal view. C. Occlusal view. ×4.

specimen was contained. The fragments of the skull recovered, part of the left premaxilla and a little of the maxilla, P^3, the right zygomatic arch, two fragments of the palatine crest, and the internal pterygoid processes, were later set into the cast (fig. 2B). The cast is incomplete, terminating immediately behind the bullae. These are very large, though not quite so large as those of *P. bicuspis;* they occupy most of the width of the basicranium, being at least 7 mm. wide and separated by about 1.5 mm. The internal pterygoid processes are long and strongly hooked

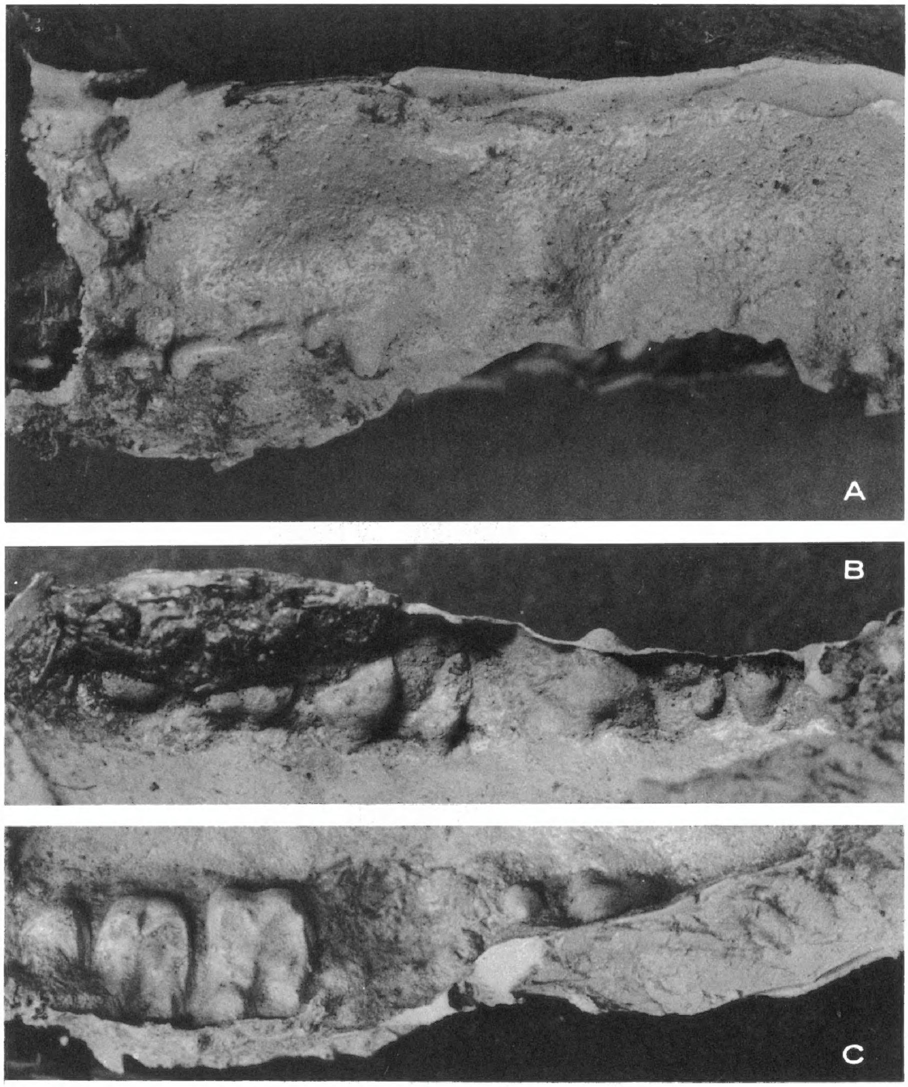

FIG. 4. *Proterix loomisi,* F:A.M. No. 74962, latex cast before addition of bone fragments, showing dentition. A. Right buccal view, showing outer sides of P^4–M^3. B. Right lingual view, showing inner sides of I^1–M^3. C. Left occlusal view, showing C–M^3. $\times 4.7$.

posteriorly. The precise size of the external pterygoid processes cannot be determined. The zygomatic arch has a maximum depth vertically of 5 mm. The palate is like that of the type except for having slightly more space between the teeth anterior to the canine; the length from the posterior edge of I^1 to the back of the palatal crest is about 22 mm.

in both. The median suture is marked by a ridge, and the groove, probably for the palatine nerve and artery, is quite plain on each side.

The right premaxilla and maxilla fragments contain I^1, which is enlarged at least as much as that of *Erinaceus,* alveoli for I^2 and I^3, and a large, two-rooted canine like that of *P. biscuspis.* P^3 has a large paracone and a small protocone.

The casts of the rest of the dentition are best seen in figure 4, large-scale photographs taken of the cast before the bone fragments were added to it. The cast shows only the lingual and buccal surfaces of the postcanine teeth and the lingual surfaces of C–I^1 on the right side; the left side shows the lingual and occlusal surfaces of the postcanine teeth. P^4 has a large paracone, strong cingulum, and a posterior prominence which almost certainly represents the end of a metastylar crest of the same form as that of *P. bicuspis.* M^1 shows a strong cingulum and, again, the buccal end of a metastylar crest. M^2 and M^3 appear only as cingula. The bases of I^2 and I^3 show that I^3 was smaller. The length cannot be determined. The cast of the canine agrees with the preserved tooth. P^2 is missing on the right, and P^3 is not clear, but shows the large paracone. P^4 shows a well-developed protocone with a poorly developed hypocone appressed to it, as in the type.

M^{1-3} are shown best in figure 4C, the left side. M^1 shows not only the same proportions as those of the type but all the important characters, including the metaconule and anterior crest of the protocone. The buccal sides of M^2 and M^3 are obscured, but the lingual sides agree with the type. P^4 is missing on the left. P^2 is shown by the cast to be a small conical tooth, as might be expected from the single small alveolus of the type.

Most of the relevant information about the rami and lower dentition (fig. 5) is given in the diagnosis. This is the only specimen of the genus showing the posterior part of the dentary. The right is the more complete, and the parts missing have been restored in plaster; the left is broken away anterior to P_4. M_1 is well preserved on the left ramus; M_1 of the right and M_2 and M_3 of both are cracked anteroposteriorly, and, although they can be seen to agree with those of *P. bicuspis,* measurements of width could not be made.

The two vertebrae (fig. 6D–G) are highly unusual. They are massive, with flat or slightly flaring, nearly square, platelike expansions on the sides, the edges of which extend above and below the bodies of the vertebrae and overlap the next vertebra posteriorly. The spine, preserved on one, is much like that of *Erinaceus,* rising about 3 mm. to or slightly above the tops of the side plates. The position of these vertebrae in the

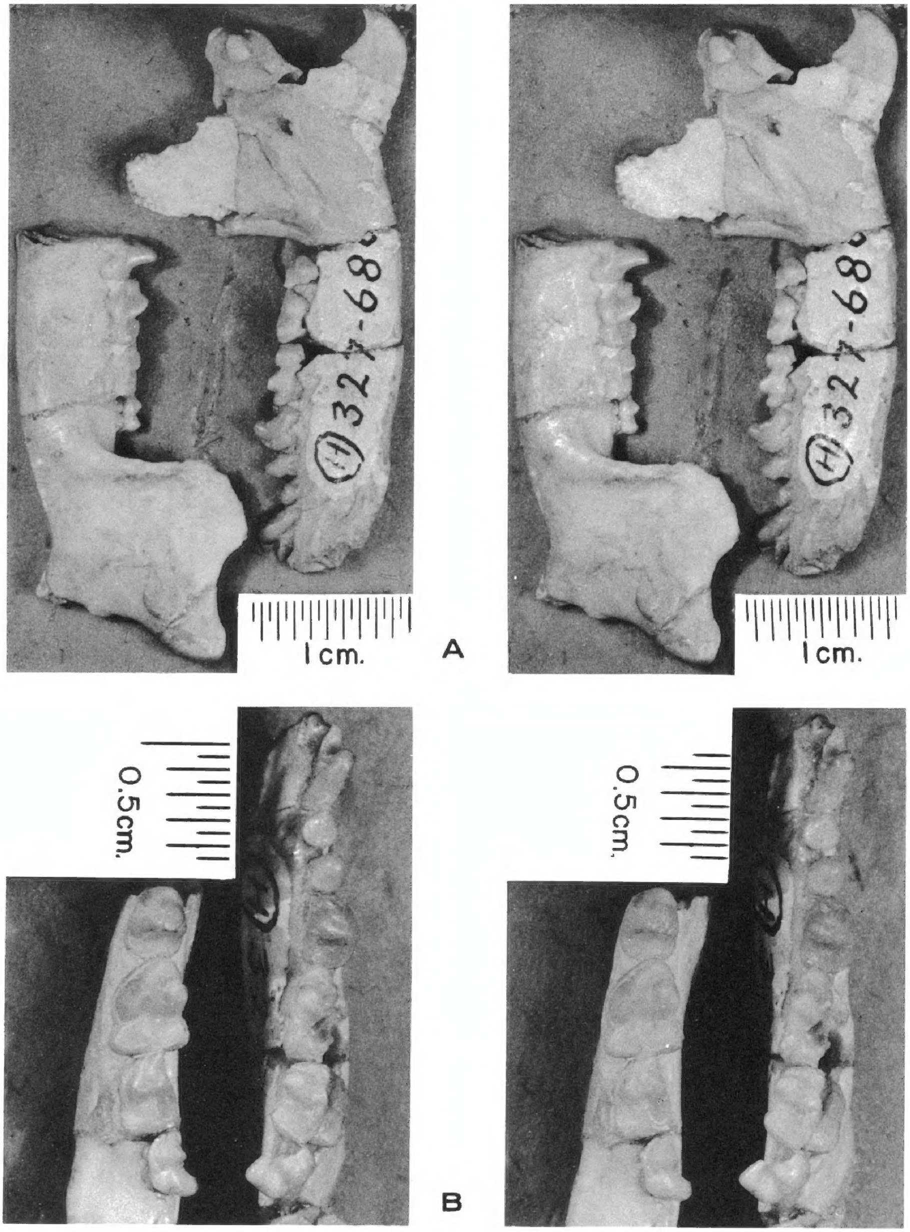

FIG. 5. *Proterix loomisi*, rami of F:A.M. No. 74962. A. Buccal view of right ramus and lingual view of left ramus. ×2. B. Occlusal views. ×3.

vertebral column is not known; their size and lack of indications of rib attachments suggest that they are lumbars.

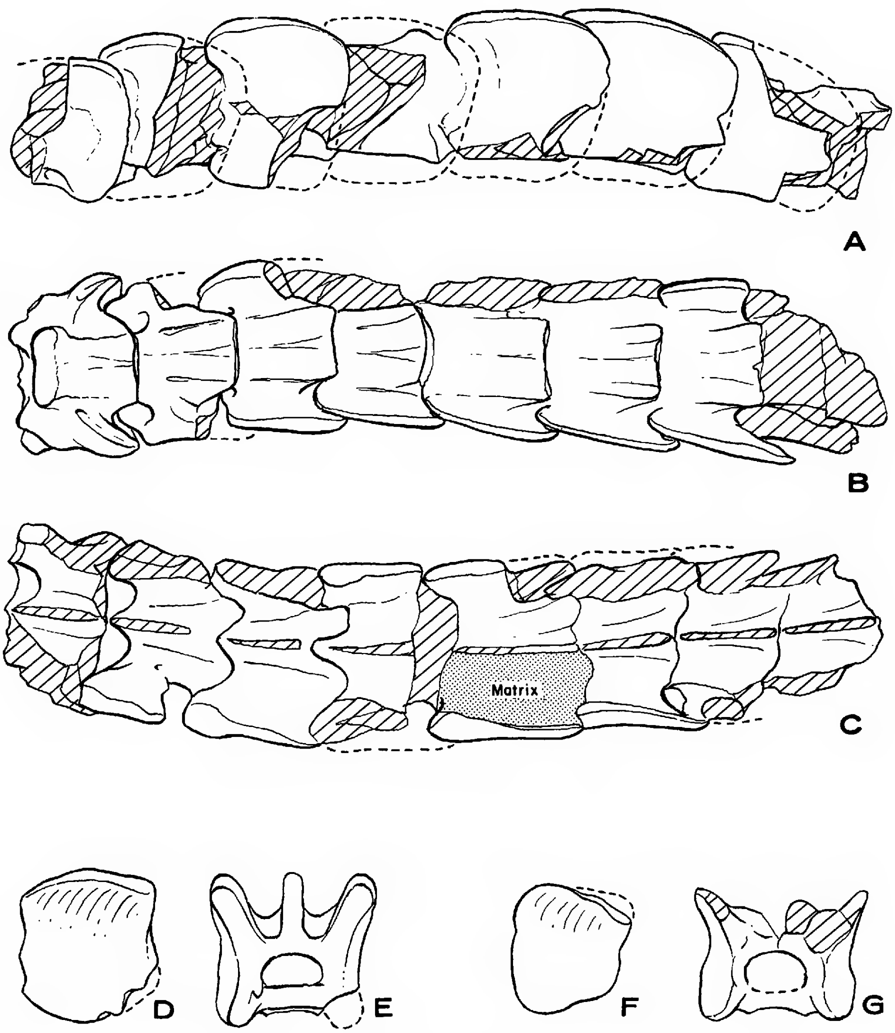

FIG. 6. *Proterix,* vertebrae. A–C. Eight ?lumbar vertebrae of *P. bicuspis,* F:A.M. No. 74961, with suggested restorations; anterior is to the left. A. Lateral view. B. Ventral view. C. Dorsal view. D–G. ?Lumbar vertebrae of *P. loomisi,* F:A.M. No. 74962, with suggested restorations. D, F. Right lateral views; anterior is to the right. E, G. Anterior views. All ×2.

Proterix bicuspis (Macdonald), new combination

TYPE: *Apternodus bicuspis* Macdonald, 1951, S.D.S.M. No. 4048.

TYPE LOCALITY AND HORIZON: "Protoceras channel sandstone, seven miles east of Rockyford, Shannon County, South Dakota" (Macdonald, 1951).

REFERRED MATERIAL: F:A.M. 74961, from "one-half mile northeast of

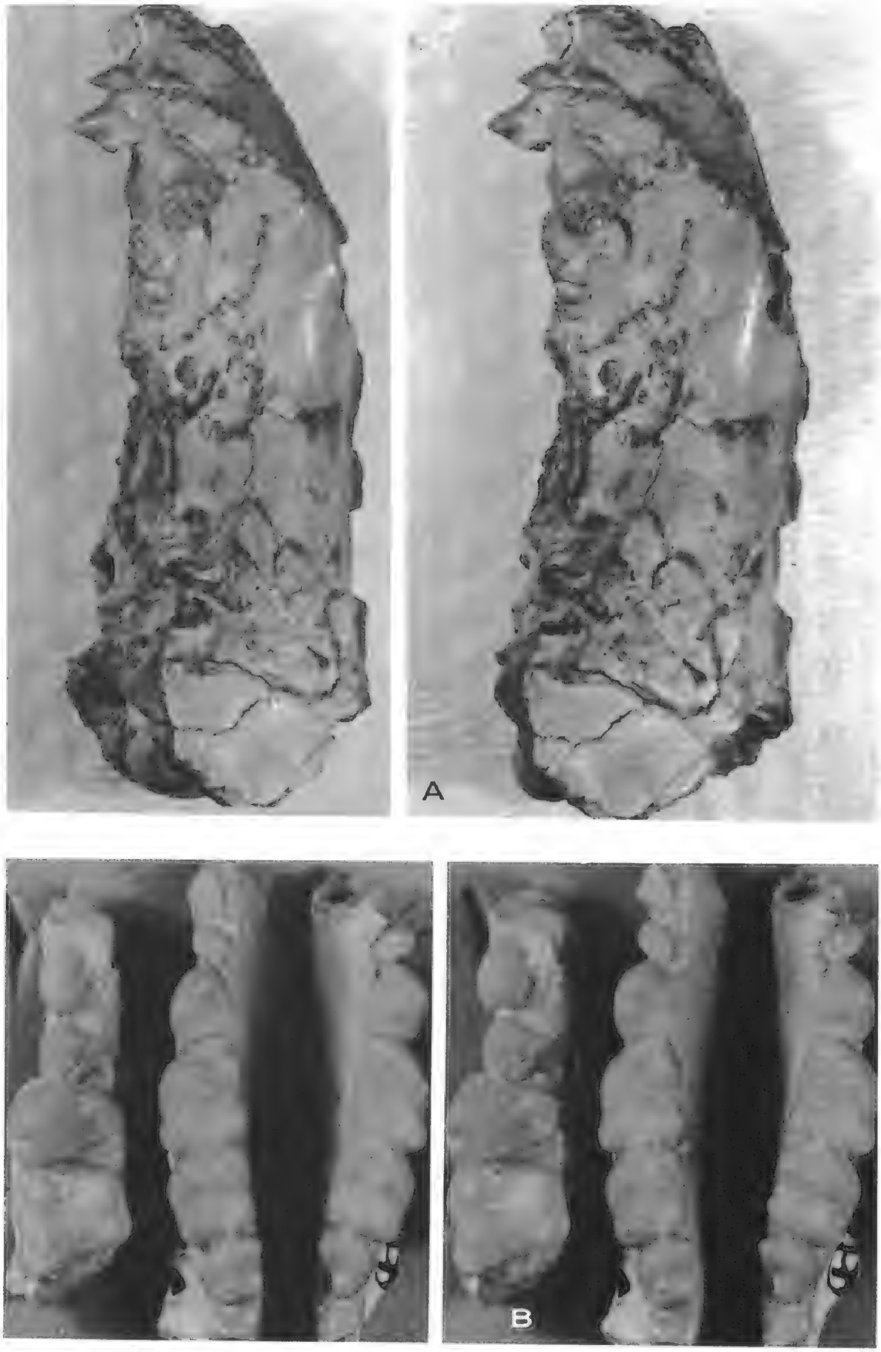

FIG. 7. *Proterix bicuspis.* A. Type, S.D.S.M. No. 4048, lateral view. ×1.8. B. F:A.M. No. 74961, two rami and partial right maxilla, with C–M^1. ×3.

Crow Butte on Ed. Franey Ranch SE. $\frac{1}{4}$, sect. 9, T.31 N., R. 51 W. Dawes County, Nebraska, 25 feet above lower ashy layer in the Whitney" (Skinner, MS).

KNOWN DISTRIBUTION: Whitneyan of Nebraska and South Dakota.

DIAGNOSIS: P^2_2 and I_3 absent; I^3 unknown; no protocone on P^3; P_3 about one-half of height of P_4; hypocone of P^4 smaller than that of *P. loomisi;* paraconid crest and talonid of P_4 smaller; M^1 longer, about as long as wide (table 1); M^2 and M^3 smaller relative to M^1; M^2 probably triangular; M^3 closer to posterior palatine crest; zygomatic arch arising opposite M^1, very deep vertically; long orbitosphenoid region; extremely large bullae.

REMARKS: The type is a partly crushed skull 5.5 cm. long, lacking the premaxillae but preserving internal casts of their posterior parts, with a damaged canine, P^3 and P^4 present, and alveoli for M^{1-3} (figs. 7A and 8).

The basicranium and left orbitotemporal region are well preserved. The area around the lacrimal foramen is damaged. A prelacrimal crest may have been present; however, the foramen appears to face outward rather than into the orbit.

The middle of the skull is elongate relative to the face. Figure 8A shows the left orbitotemporal region. The bone lateral to the alisphenoid canal, which is extremely long, is broken away, showing an internal cast; on the right the canal is completely covered. The optic foramen is anterior to the suboptic foramen, a position attributed by Butler (1948, p. 454) in *Echinosorex* to the elongation of the orbitotemporal region (however, *Brachyerix,* with a short orbitotemporal region, shows the same condition). As in other erinaceids, a crest extends from the top of the sphenorbital foramen upward and anteriorly, showing the position of the septum behind the orbit (Butler, 1948, p. 454). Along the orbitosphenoid-frontal suture are three major foramina, and possibly two minor ones. They probably carried two branches of the lateral cerebral vein and an artery, as in *Erinaceus* (Butler, 1948, p. 457). The squamosal portion of the zygomatic arch is known from a mold of the medial surface on a fragment of matrix. This also preserves an impression and fragments of the side of the skull and of the base of the arch itself, and can be fitted precisely to the skull. The arch was much higher and deeper vertically than in other erinaceids. At its junction with the skull, the lower edge is in the same position as in other forms, but the upper edge is nearly as high as the sagittal crest. The vertical depth of the arch is about 9 mm.; the maximum height of the skull is only 18 mm. The base of the arch includes much of the lateral exposure of

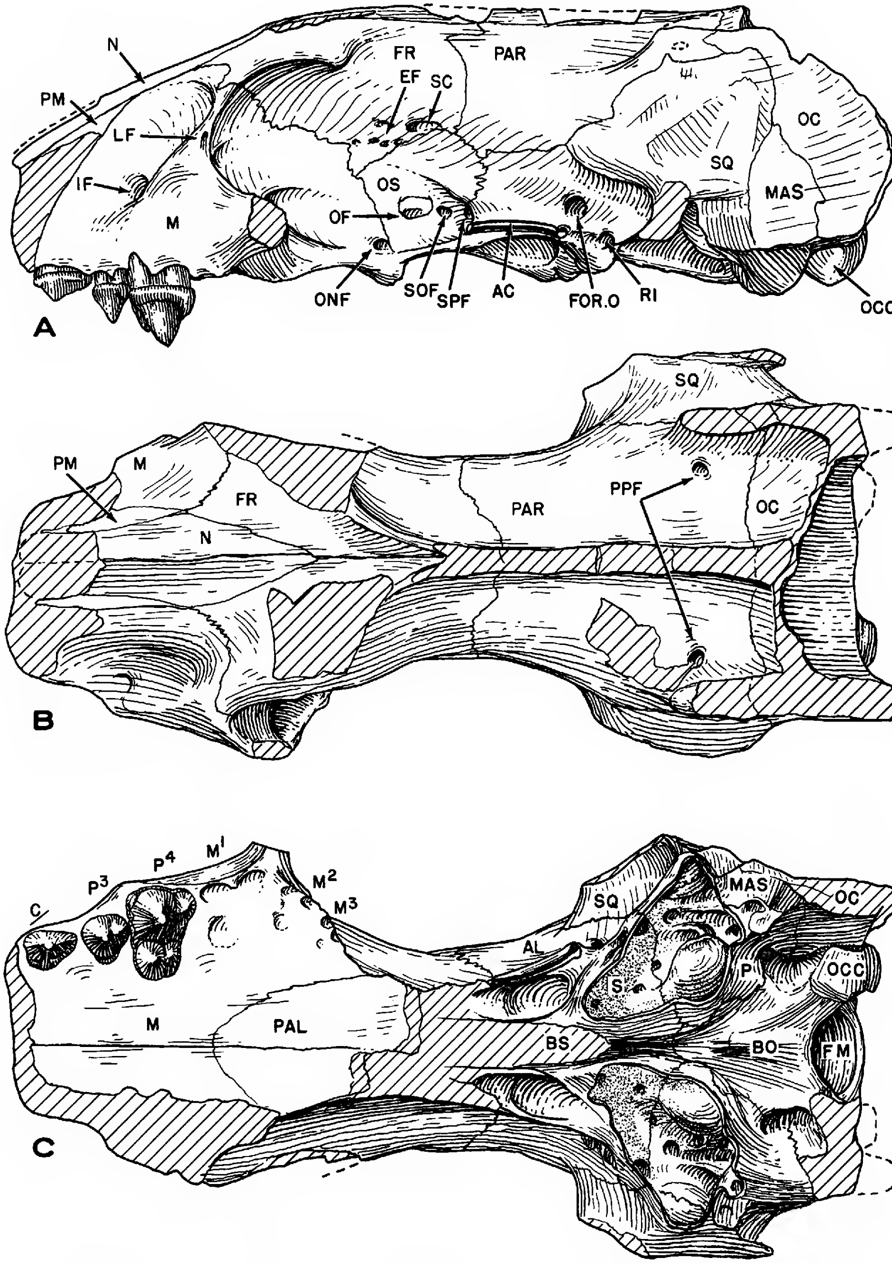

FIG. 8. *Proterix bicuspis,* type, S.D.S.M. No. 4048. A. Lateral view. B. Dorsal view. C. Ventral view. All ×2.

Abbreviations: AC, alisphenoid canal; AL, alisphenoid; BO, basioccipital; BS, basisphenoid; EF, ethmoid foramen; FM, foramen magnum; FOR.O, foramen ovale; FR, frontal; IF, infraorbital foramen; LF, lacrimal foramen; M, maxilla; MAS, mastoid; N, nasal; OC, occipital; OCC, occipital condyle; OF, optic foramen; ONF, orbitonasal foramen; OS, orbitosphenoid; P, petrosal; PAL, palatine; PAR, parietal; PM, premaxilla; PPF, postparietal foramen; RI, foramen for ramus inferior of stapedial artery; S, sphenoid; SC, sinus canal; SOF, suboptic foramen; SPF, sphenorbital foramen; SQ, squamosal.

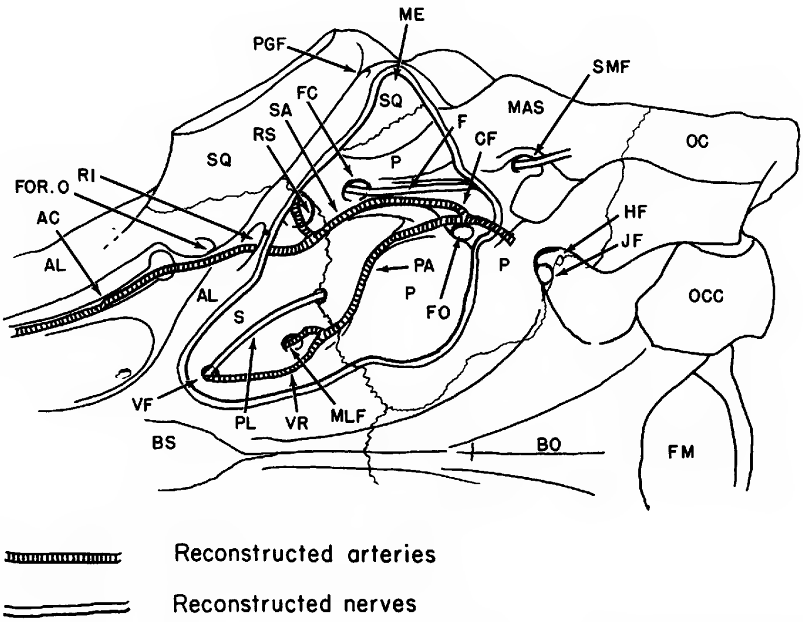

FIG. 9. Diagram of basicranium of *Proterix bicuspis*, type, S.D.S.M. No. 4048, with reconstruction of arteries and nerves of the tympanic region. ×4.

Abbreviations: AC, alisphenoid canal; AL, alisphenoid; BO, basioccipital; BS, basisphenoid; CF, carotid foramen; F, facial branch of nerve VII; FC, Fallopian canal; FM, foramen magnum; FO, fenestra ovalis; FOR.O, foramen ovale; HF, hypoglossal foramen; JF, jugular foramen; MAS, mastoid; ME, meatus; MLF, middle lacerate foramen; OC, occipital; OCC, occipital condyle; P, petrosal; PA, promontory artery; PGF, postglenoid foramen; PL, palatine branch of nerve VII; RI, foramen for ramus inferior of stapedial artery; RS, foramen for ramus superior of stapedial artery; S, sphenoid; SA, stapedial artery; SMF, stylomastoid foramen; SQ, squamosal; VF, Vidian foramen; VR, Vidian ramus of promontory artery.

the squamosal, and is grooved posteriorly so that a flaring edge projects posteriorly, subparallel to the lambdoid plate, and about 3 mm. lateral to it. The arch narrowed anteriorly; its base on the maxilla is low and only 3 mm. wide. The position of the impression suggests that the arch was crushed inward during compaction of the sediments.

A strong sagittal crest is present, largely broken in this specimen, but its shape indicates a very straight dorsal profile (fig. 8A, B). The frontal-parietal suture has a small forward curve, but the parietal does not have a long process extending toward the maxilla as in *Hylomys*. The strong occipital crest appears to be made up entirely by the occipital bone; however, the absence of evidence of an interparietal may be due to damage. A large postparietal foramen is present, presumably

carrying a branch of the external jugular vein as in *Erinaceus* (Butler, 1948, p. 457). The rugosity of the skull roof noted by Butler (1948, p. 471) in *Neurogymnurus* is detectable but not pronounced.

The lateral plates (fig. 8) are vertical, quite flat except for the bases of the arches, and extend well behind the occipital condyles. Both are broken along the entire length of their edges from the occipital crest to the lower edge of the mastoid, so that their full extent is unknown. The occipital crest extends laterally and slightly posteriorly and terminates at the tops of the plates. The posterior lambdoid crest is extremely strong, forming the posterior edge of the plate. Because the plates are largely bounded by the posterior lambdoid crest, I have called them "lambdoid plates." The term "auditory plates" used by Schlaikjer (1933) and others for similar structures is misleading, since they have no known auditory function. The term here proposed avoids any functional interpretation and also does not specify which bones are involved or to what extent.

The anterior lambdoid crest cannot be identified and is probably absent. The anterodorsal edge of the plate, nearly as high as the sagittal crest, parallels it forward and dies out above the external auditory meatus. The squamosal is extended far up the plate but not posteriorly. The mastoid exposure is narrow and terminates in a point at about two-thirds of the height of the squamosal. The back and top of the plate are formed by a large lateral exposure of the occipital. The effect of the nearly horizontal occipital crest and vertical plates is to give the back of the skull a nearly rectangular cross section, with the sagittal crest little higher than the posterior lambdoid crests.

The tympanic region (figs. 8C, 9, 10) is extremely well preserved and very similar to that described by Butler (1948, p. 455, 472) for *Neurogymnurus*. All structures described below can be seen in both bullae. The bullae are very large and close together, occupying most of the width of the basicranium. Anteriorly they are less than 1 mm. apart, compared to maximum lengths and widths of the bullae of 10 mm.

The bulla is made up of wings of the alisphenoid, basisphenoid, and periotic. The squamosal has a process downward on each side of the meatus, enclosing a notch about 3 mm. high reaching nearly to the roof of the bulla. The extent of the tympanic contribution to the bulla is unknown. The floor of the bulla is broken away on each side, leaving a wall at least 1.5 mm. high, continuous except for the meatus. These are all broken edges except for the squamosal and alisphenoid lateral to the foramen for the ramus inferior of the stapedial artery (see below). It would appear, then, that the bullar wings of the surrounding bones

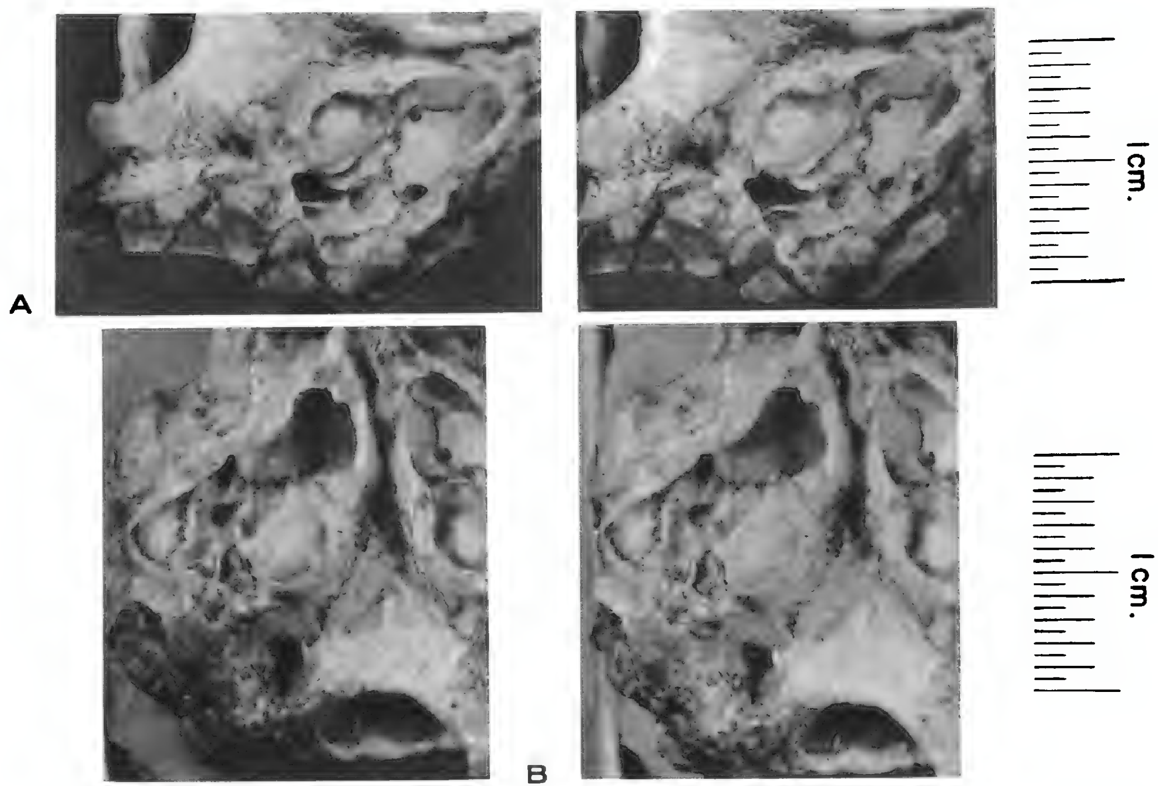

FIG. 10. *Proterix bicuspis,* type, S.D.S.M. No. 4048. A. Left bulla. B. Right bulla. ×2.8.

were more extensive than in modern erinaceids, and that the squamosal and alisphenoid formed an unusually high ridge laterally. The large periotic wing is notable. That of *Echinosorex* is smaller, and modern members of the Erinaceinae have none.

The roof of the bulla is quite similar to that of *Neurogymnurus,* made up of the periotic, sphenoid (no suture is visible between the alisphenoid and basisphenoid), and squamosal. The sphenoid-periotic suture crosses the bulla transversely and cuts the medial wall at the basioccipital-basisphenoid suture. The periotic-basioccipital suture slants posterodorsally along the medial side of the bullar wall in such a way that a low basioccipital wing is present on the outside, but not the inside, of the bulla.

The arteries of the tympanic region followed the same pattern as in *Erinaceus* (Butler, 1948, pp. 454–456). The internal carotid artery entered the bulla through a notch or foramen in the same position as in *Erinaceus* (fig. 9). Grooves on the promontorium and bullar roof show the positions of the promontory and stapedial arteries. The middle lacerate foramen is in the sphenoid just anterior to the suture with the periotic. A large foramen for the ramus superior of the stapedial artery lies in the sphenoid laterally, just anterior to the squamosal-periotic suture. The ramus inferior left the bulla through a foramen in the alisphenoid, then followed a groove into the long alisphenoid canal. The posterior opening of the Vidian canal is in the anterior end of the sphenoid, and probably carried a branch of the promontory artery as as well as the palatine branch of the seventh nerve.

This nerve left the cranium through a foramen in the sphenoid-periotic suture just lateral to the middle lacerate foramen. The facial nerve left the Fallopian canal by a foramen in the groove for the stapedial artery, somewhat anterior to its position in *Erinaceus.* The stylomastoid foramen is in the same position as in *Erinaceus;* the facial nerve probably followed the large groove carrying the stapedial artery. Depressions in the periotic on each side of this groove show the positions of the attachments of the stapedial and tensor tympani muscles.

There is no basisphenoid pit. The hypoglossal foramen is not set in an emargination of the condyle, but posterior to the jugular foramen in a depression on the periotic-basioccipital suture. The paroccipital process continues posterior to the condyle, forming the lower edge of the lambdoid plate. The ventral side of the condyle appears to be directed anteroposteriorly, parallel to the plates, rather than diagonally as in other erinaceids. The foramen magnum is a low oval, not rising above the condyles. Internal and external pterygoid processes were present, but

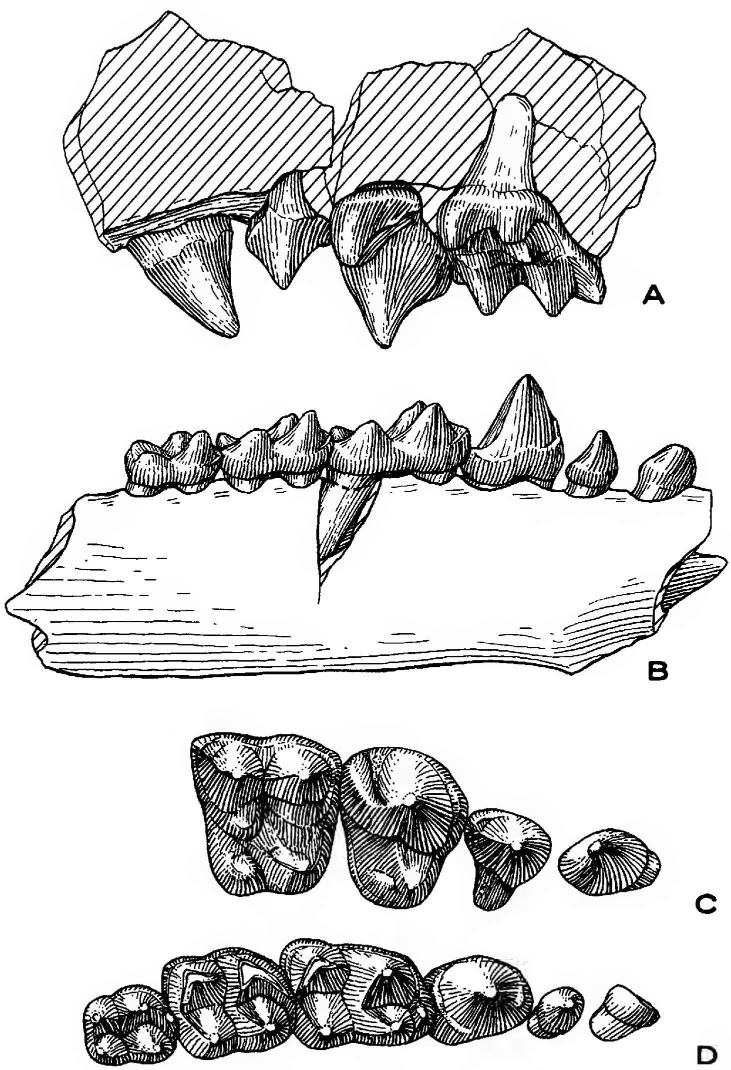

FIG. 11. *Proterix bicuspis,* F:A.M. No. 74961, fragment of right maxilla, with C-M^1, and left ramus, with C-M_3 and root of I_1. A. Lingual view of maxilla. B. Lingual view of ramus. C, D. Occlusal views. $\times 4$.

are broken away. A small venous foramen (Butler, 1948, p. 456) is present in the alisphenoid between them.

The other specimen here referred to this species consists of a right maxillary fragment, two rami, and eight vertebrae from the Whitney of Dawes County, Nebraska (figs. 6A-C, 7B, and 11). The maxilla, which has M^1-C, is assigned to this species on the basis of the shape of M^1 (see table 1); the close correspondence of P^4 to that of the type,

especially the poorly developed hypocone and short, nearly transverse metastylar crest; the three-rooted P^3 without a protocone; and the lack of P^2. The two rami match in size, and the right occludes properly with the maxilla, confirming that they are from one individual. The rami contain M_3–C and the base, in one, and an alveolus, in the other, for a large I_1. The left also shows the alveolus of a smaller incisor, presumably I_2. As noted above, M^1, like the alveolus of the type specimen, is nearly as long as wide, unlike *P. loomisi.* It also shows a crest extending anterolingually from the paracone which is not apparent in *P. loomisi,* but this difference is very likely due to the greater extent of wear in *P. loomisi.*

The eight vertebrae (fig. 6A–C) are like those of *P. loomisi.* They are articulated and show an average overlap of the side plates of about 2 mm. All the spines except the posterior half of the fifth are broken off; the part remaining is 3 mm. high, about the same as the spines of *Erinaceus.* The lengths of the vertebrae, also, are about the same as those in *Erinaceus,* increasing posteriorly from 6 mm. to 7 mm. through the length of the lumbar series.

DISCUSSION

Whereas M^1 is larger and longer in *Proterix bicuspis* than in *P. loomisi,* M^2 is smaller and set farther inward. It may have had a similar shape, but the more lingual position of the posterobuccal root suggests a more triangular outline (fig. 8C). M^3 is even smaller relative to M^2, set farther inward, and the posterobuccal root is nearly posterior to the lingual root. The effect of these differences can be seen by comparing figures 1A and 8C. The outline of the tooth row in *P. loomisi* is straight lingually and a smooth curve buccally, but *P. bicuspis* has the inner side of M^3 lingual to that of M^1, and a sharp break and inward angle after M^1 buccally. M^1 extends farther back and outward, so that its posterobuccal root encroaches slightly on the base of the zygomatic arch. The arch arises almost entirely opposite M^1, as in *Erinaceus;* in *P. loomisi* it arises almost entirely opposite M^2. The posterior edge of the palate has a sharper inward angle in *P. bicuspis,* and the two posterior molars seem to have been pushed back and in along it as M^1 expanded and migrated posteriorly.

To sum up, *P. bicuspis* has a shorter face and tooth row and fewer, simpler teeth, with M^1 increased in size and functional importance. The orbitosphenoid region, on the other hand, is much longer. Since, judged by the specimens on hand, *P. bicuspis* is a slightly larger form, some of this difference may be due to allometric factors.

The vertebrae appear to be similar in the two species. The only form known that has vertebrae similar to these is *Scutisorex* Thomas, which has curved lateral expansions bearing interlocking spines on the dorsal and lumbar vertebrae (Allen, 1917). In this case, the number of lumbars is increased. *Erinaceus* has seven lumbars. The last of the eight of *P. bicuspis* is too damaged to show whether it was a lumbar or a sacral. Allen's figures of *Scutisorex* indicate that the lengths of the individual vertebrae were reduced. As noted above, those of *P. bicuspis* are as large as those of *Erinaceus,* but the skull sizes indicate that *Proterix* was smaller. It is unlikely, therefore, that the number of lumbars was increased. The modifications of the vertebrae of *Scutisorex* appear to make the spine relatively rigid (though, as noted by Allen, the effects on the movements of the living animal do not appear to be so drastic as would be expected from a study of the skeleton). The plates of *Proterix* appear to permit free vertical movement, but very little lateral movement and twisting. It is interesting to note that *Scutisorex* also has a greatly expanded mastoid area, with a strong posterior lambdoid crest and roughening of the skull roof. A functional explanation for the peculiar structure of the spinal column of *Scutisorex* has not yet been found. A detailed study of the functional morphology of these forms, and particularly of the musculature of the vertebral column and jaws, is needed, but is beyond the scope of this paper. The massive construction of the back of the skull, zygomatic arches, and jaw suggests a powerful bite.

Comparison was made with several specimens of *Galerix exilis* from the Miocene of France. This genus possesses longer jaws and the complete primitive dentition, as in recent members of the Echinosoricinae. I_1 is at least as large as I_2, and I_3 may be small. The lower canine may have been somewhat broader at the base. P_1 is present; P_2 is two-rooted, with traces of a paraconid and talonid; P_3 can be nearly as large as P_4, and is two-rooted, with a large protoconid, small paraconid, metaconid crest, and talonid; P_4 has a three-cusped trigonid, with a distinct talonid bearing a hypoconid; M_{1-3} show a better development of the paraconid, and the talonid of M_3 is wider. The upper incisors could not be compared. P^1 is small and simple; P^2 has a large paracone, with an anterior cingulum and a slight metastylar crest; P^3 possesses a large paracone, with a metastylar crest, anterior cingulum, and well-developed and well-separated protocone and hypocone; P^4 has a smaller paracone, larger metastylar crest, and well-separated protocone and hypocone. M^1 and M^2 resemble those of *P. loomisi* in shape, but have better-developed metastylar crests, metaconules, and parastyles. Parastyles are faint in or absent from *Proterix.* M^3 is much like that of *P. loomisi,* but

the posterobuccal root is almost directly behind the anterobuccal root. In *P. loomisi* the posterobuccal root and the metacone are more lingual. In *P. bicuspis* the posterobuccal root is almost directly behind the lingual root, and the posterobuccal root of M^2 has moved inward to approximately the position of that of M^3 in *P. loomisi.*

Comparison with *Amphechinus* shows two important differences which separate this and other members of the Erinaceinae from *Proterix:* the perforation of the palate and the enlargement of I_2.[1] Examination of F:A.M. No. 74962 leaves no doubt that the enlarged incisor here was I_1, and that I_3 was the one lost in *P. bicuspis.*

Neurogymnurus, as described by Butler (1948), shows some resemblances to *Proterix,* as well as important differences. It is more brachycephalic; the nasals are not exceptionally long; the lacrimal foramen opens into the orbit, and a prelacrimal crest was probably present. An alisphenoid canal is present, moderately long for an erinaceid, but much shorter than that of *P. bicuspis.* The optic foramen is directly above the suboptic foramen. Two foramina are present at the frontal-orbitosphenoid suture. Butler interpreted the larger as the "ethmoid" foramen for the lateral cerebral vein (sinus canal of other authors, discussed by McDowell, 1958, p. 128) and the other as carrying the associated artery or a branch of the vein. The zygomatic arch is narrow and low posteriorly, widening anteriorly. The interparietal is triangular. Weak temporal crests are present in place of a sagittal crest. The most important differences are in the posterolateral areas of the skull; the squamosal in *Neurogymnurus* extends to the back of the skull, reducing the mastoid to a low, horizontal exposure, and excluding the occipital completely from the side of the skull. The occipital crest divides low on the skull, and the anterior lambdoid crest is very weak and nearly horizontal. The posterior crest is very strong. The back of the skull has a rounded cross section.

The bullae are smaller, with a relatively smaller periotic wing. The tympanic is known; it makes up a significant part of the bulla. Other details of the tympanic region are nearly identical. The hypoglossal foramen is set in an emargination of the condyle. The paroccipital process is continuous with the side of the skull and projects backward, but not posterior to the condyle, and the occipital component does not extend posterior to the mastoid.

The teeth of *Neurogymnurus* were figured and discussed by Leche (1902).

---

[1] The view held by Butler and earlier workers that the enlarged lower incisor of erinaceines is I_2, I_1 being lost, is based on embryological studies on *Erinaceus.* McKenna and Holton (1967) have suggested, on the basis of undescribed specimens of *Tupaiodon* and *Palaeoscaptor,* that the enlarged incisor is I_1.

As does *Galerix,* it has the full primitive dentition, $\frac{3\,1\,4\,3}{3\,1\,4\,3}$. P^1 and P^2 are two-rooted. P^3 is three-rooted, with a protocone and a metastylar crest. P^4 has a longer metastylar crest and a stronger hypocone than does that of *Proterix.* M^1 has a longer metastylar crest, is shorter anteroposteriorly, and has a more irregular outline owing to a narrower cingulum. M^2 is similar and very little smaller. M^3 is triangular but larger than in *Proterix.* Butler observed that the zygomatic arch arises opposite M^2.

P_3 has a talonid; P_4 has a larger talonid than does that in *Proterix,* with a crest or hypoconid posteriorly; M_1 has a larger paraconid; M_2 and M_3 (Leche, 1902) are similar to those teeth in *Proterix.* The mental foramen is below the anterior root of P_3 (Butler, 1948).

Comparison could not be made with *Proterixoides davisi* Stock, 1935.[1]

Brachyerix of the middle Miocene and *Metechinus* of the lower Pliocene are very brachycephalic forms. McKenna and Holton (1967) have recently placed *Dimylechinus* and a new Mongolian genus with them in Butler's tribe Brachyericini, which they have raised to subfamily rank. These all have three or fewer procumbent, single-rooted teeth between the enlarged incisor and P_4. *Brachyerix* has two or possibly three upper premolars. P^3 has three roots and a single cusp. P^4 has a paracone, a long metastylar crest, a low protocone, and no hypocone. M^1 has no metaconule and a long metastylar crest. M^2 resembles M^3 of *P. loomisi,* and M^3 is absent. The back of the palate turns in more sharply than in *P. bicuspis.*

The alisphenoid canal of *Brachyerix* is represented by a groove. The optic foramen is anterior to the suboptic foramen. The zygomatic arch is narrow and low, and arises opposite M^1. The side of the skull and posterior lambdoid crest resemble those of *Neurogymnurus,* but faint sutures indicate that the squamosal is not extended back. The bullae are as large as those of *P. bicuspis,* and almost completely covered by wings of the surrounding bones, including a very large periotic wing. The tympanic contribution was apparently small. The carotid artery and its branches were enclosed in bony tubes (McKenna, 1966). There are no palatine vacuities or basisphenoid pit. The nasals reach the postorbital process.

---

[1] The type specimen of this species has been lost, as have also the original illustrations. The measurements given for *Proterix loomisi* vary greatly from those obtained by Matthew (1903) and by myself, and some are clearly impossible. Those for *Proterixoides* appear to be equally unreliable, M^1 being given as longer than wide, contradicting the published illustration.

STRATIGRAPHY

As mentioned above, all the specimens of *Proterix* are Whitneyan in age. Of the two Nebraska specimens, F:A.M. No. 74962 (*P. loomisi*) was found at least 65 feet below the lower ash of the Whitney member of the Brule Formation and F:A.M. No. 74961 (*P. bicuspis*), 25 feet above the same ash. Of the South Dakota specimens, the type of *P. loomisi* (A.M.N.H. No. 9756) was found in the upper Oreodon beds, which form the lower Poleslide member of the Brule Formation as defined by Bump in 1956. The ramus of *P. loomisi,* S.D.S.M. No. 55140, was found high in the Leptauchenia nodules of the middle Poleslide member. The horizon of the type specimen of *P. bicuspis,* S.D.S.M. No. 4048, was given only as the Protoceras channel sandstone, which occurs at several levels through the middle Poleslide member. The Whitney and Poleslide are considered equivalent; the lower ash of the Whitney correlates within the lower Poleslide (upper Oreodon beds). The species are thus contemporaneous, with the oldest and probably the youngest specimens being *P. loomisi.*

CONCLUSIONS

To sum up, there appears to be a close relationship between *Proterix loomisi* and the species hereby transferred to the genus. Though the known specimens are essentially contemporaneous, *P. bicuspis* is more extreme compared with other early erinaceids in the simplification of the dentition, the size of the zygomatic arch, the size of the bulla, and probably in the massiveness of the back of the skull, and is probably a descendant of *P. loomisi.* The position of *Proterix* has long been a problem (see, for instance, McKenna and Simpson, 1959). It does not fit well into any of the subfamilies recognized by Butler (1948). The dentition is typified mainly by tooth reduction, migration, and loss during the shortening of the face. The high specialization of the back part of the skull suggests a long separate development. *Proterix* could have developed from the pre-Oligocene stock of any of the subfamilies. It seems best at this time to leave *Proterix* as an isolated genus.

Proterix seems far too specialized to have given rise to *Brachyerix* and *Metechinus,* and an earlier member of the same group is known from Mongolia (McKenna and Holton, 1967). These forms, however, show great parallelism in the reduction of the dentition, the enlargement of the bullae, and the strong development of the lambdoid crest. They suggest that the enlargement of M^1 and its backward migration relative to the zygomatic arch and the reduction and triangular shape of M^2,

which are directly related to the shortening of the face, and the strong development and backward projection of the lambdoid crest all result from a single cause, probably connected with a change in the form and function of the musculature of the jaws and neck, and, at least in *Proterix,* of the vertebral column as well.

REFERENCES

ALLEN, J. A.
1917. The skeletal characters of *Scutisorex* Thomas. Bull. Amer. Mus. Nat. Hist., vol. 37, pp. 769–784, figs. 1–8, pls. 89–92.

BUMP, JAMES D.
1956. Geographic names for members of the Brule Formation of the Big Badlands of South Dakota. Amer. Jour. Sci., vol. 254, pp. 429–432.

BUTLER, P. M.
1948. On the evolution of the skull and teeth in the Erinaceidae, with special reference to fossil material in the British Museum. Proc. Zool. Soc. London, vol. 118, pt. 2, pp. 446–500, figs. 1–28, tables 1–2.

LECHE, WILHELM
1902. Zur Entwicklungsgeschichte des Zahnsystems der Säugethiere. Theil II: Phylogenie. Heft I: Die Familie der Erinaceidae. Zoologica, Stuttgart, no. 37, pp. 1–103, figs. 1–59, pls. 1–4.

MACDONALD, JAMES REID
1951. Additions to the Whitneyan fauna of South Dakota. Jour. Paleont., vol. 25, pp. 257–265, figs. 1–4, tables 1–3.
1961. The lower dentition of *Proterix loomisi* Matthew? *Ibid.,* vol. 35, pp. 632–633, fig. 1, 1 table.
1963. The Miocene faunas from the Wounded Knee area of western South Dakota. Bull. Amer. Mus. Nat. Hist., vol. 125, pp. 139–238, figs. 1–30, tables 1–31, 2 maps.

MCDOWELL, SAMUEL BOOKER, JR.
1958. The Greater Antillean insectivores. Bull. Amer. Mus. Nat. Hist., vol. 115, pp. 117–214, figs. 1–46, tables 1, 2.

MCKENNA, MALCOLM C.
1966. Paleontology and the origin of the primates. Folia Primatologica, vol. 4, no. 1, pp. 1–25, figs. 1–10.

MCKENNA, MALCOLM C., AND CHARLOTTE P. HOLTON
1967. A new insectivore from the Oligocene of Mongolia and a new subfamily of hedgehogs. Amer. Mus. Novitates, no. 2311, pp. 1–11, figs. 1, 2.

MCKENNA, MALCOLM C., AND GEORGE GAYLORD SIMPSON
1959. A new insectivore from the middle Eocene of Tabernacle Butte, Wyoming. Amer. Mus. Novitates, no. 1952, pp. 1–12, fig. 1, table 1.

MATTHEW, W. D.
1903. A fossil hedgehog from the American Oligocene. Bull. Amer. Mus. Nat. Hist., vol. 19, pp. 227–229, fig. 1.

MATTHEW, W. D., AND C. C. MOOK
1933. New fossil mammals from the Deep River Beds of Montana. Amer. Mus. Novitates, no. 601, pp. 1–7, figs. 1–2.

SCHLAIKJER, ERICH M.
1933. Contributions to the stratigraphy and paleontology of the Goshen Hole area, Wyoming. I. A detailed study of the structure and relationships of a new zalambdodont insectivore from the middle Oligocene. Bull. Mus. Comp. Zool., vol. 76, no. 1, pp. 1–27, figs. 1–8, 1 pl.

SKINNER, MORRIS F.
[MS.] Frick Laboratory field notes and section book. Frick Laboratory, the American Museum of Natural History.

STOCK, CHESTER
1935. Insectivora from the Sespe uppermost Eocene, California. Proc. Natl. Acad. Sci., vol. 21, no. 4, pp. 214–219, pl. 1.